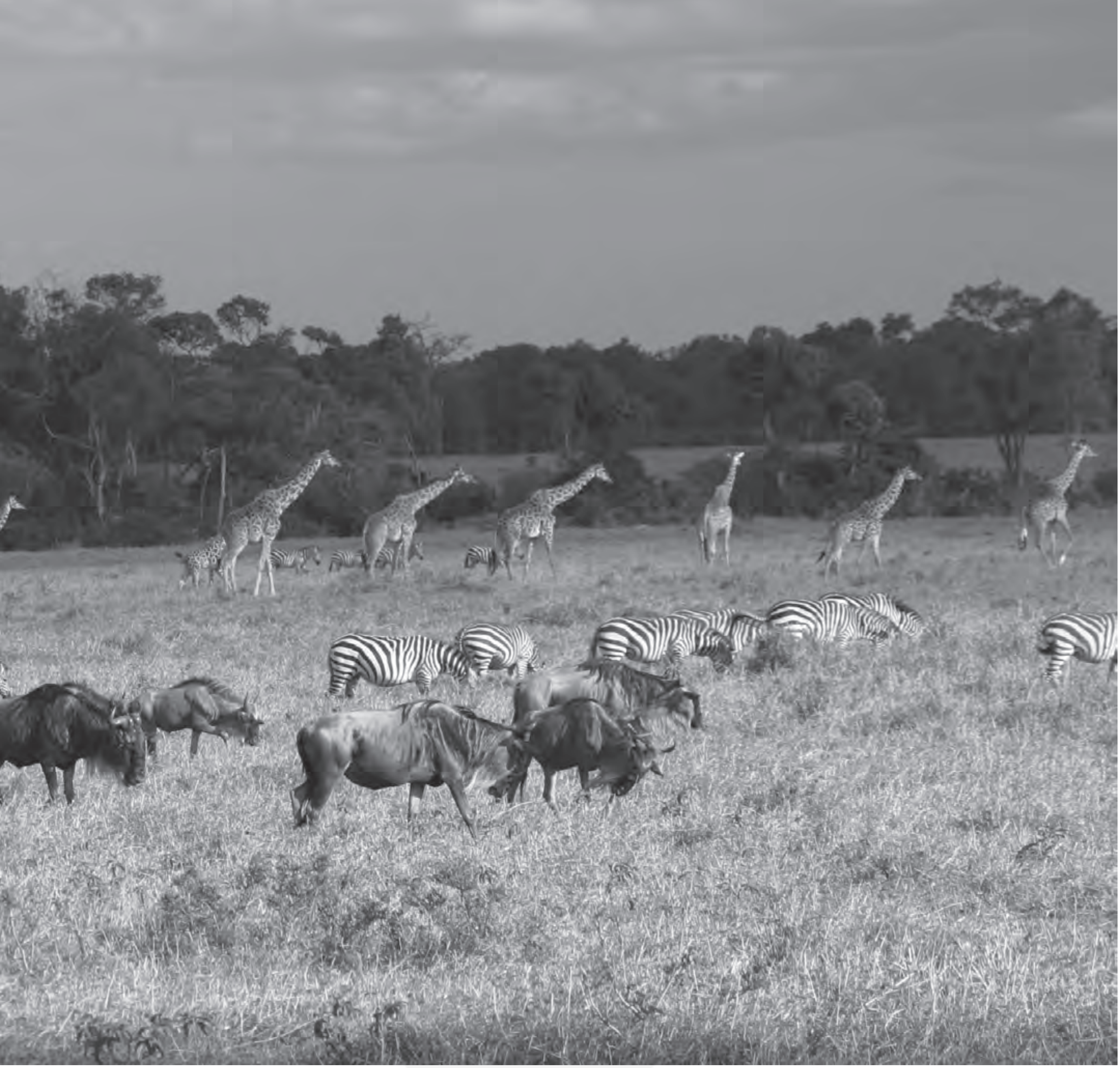

Ungulate Taxonomy

COLIN GROVES and PETER GRUBB

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Preface

IT HAS NOW been nearly a century since the last major survey of ungulate taxonomy appeared (Lydekker, 1913, 1915a, b; Lydekker & Blaine, 1914a, b). A new treatment would be needed only if, in the meantime, there have been major advances in knowledge and understanding; and indeed there have. This is our first major justification for writing this new book.

In most biota, ungulates are among the most visible fauna on the landscape. In national parks they are readily spotted and much admired by visitors, and it is easy to assume that because these animals are so familiar, everything is known about them, especially how many species there are. Such an assumption would be wrong. Mammalogists expect diversity among small mammals, and seek it out, but they have grown used to accepting that larger ones, because they are thought to be highly mobile (and indeed they may be), are bound to be much less diverse and thus will yield up less information about ecosystems, biogeography, and so on. It may be taken for granted that an antelope of a particular "kind" is, to an extent, expendable: if it becomes endangered in one place, replacements can be found elsewhere and imported in order to top up the local gene pool—such, at any rate, is the assumption, but it needs to be tested: are the local gene pools really exchangeable, or are some of them unique? Taxonomy can go some way toward testing such propositions.

The coming of the molecular revolution has begun to reopen such questions, but morphological research has often not kept up. Because both of us have been traditional skin-and-skull taxonomists, we felt that this was a gap that must be filled, and it was only by going through the different ungulate groups, one by one, that we would find out exactly which gaps remained to be filled, and what research still needed to be done.

We do not intend to present this book as a finished proposition. Time and again, we remark that "more research is necessary"; we want, above all, to stimulate more taxonomic research on ungulates. In some cases we have been able to break new ground, and we hope that these examples will be examined by colleagues and, if found acceptable, used as templates for other studies.

We have both benefited enormously from the assistance of museum curators, discussions with colleagues, and help and advice from families and friends—going back at least 40 years. We would like to take this opportunity to thank (in alphabetical order): Alexei Abramov, Faris Al-Timimi, Renate Angermann, Bruce Banwell, Kurt Benirschke, the late Biswamoy Biswas, Boeadi, Gennady Boeskorov, Peter van Bree, Isabella Capellini, Sujit Chakraborty, Lucas Chin, Bill Clark, Cäsar Claude, Juliet Clutton-Brock, Gordon Corbet, Loïc Costeur, Woody Cotterill, the late Peter Crowcroft, Jacques Cuisin, the late Pierre Dandelot, J. C. Daniel, Bijan Dareshuri, Shantini Dawson, Jim Dolan, Keith Dunmall, Feng Zuojiang, Pruthu Fernando, Wolfgang Frey, Val Geist, Alan Gentry, Anthea Gentry, Arnaud Greth, David Happold, Malcolm Harmon, David Harrison, Larry Heaney, Kris Helgen, Mahmoud Reza Hemami, Helmut Hemmer, Daphne Hills, the late John Hill, Kes Hillman, the late Dick Hooijer, Barry Hughes, Paula Jenkins, the late Peter Jewell, Tolga Kankiliç, Mahmoud Karami, Christian Kern, Jonathan Kingdon, Steve Kingswood, Dieter Kock, Katrin Kohmann, Richard Krafft, the late Arlene Kumamoto, Adrian Lister, Ibnu Maryanto, Frieder Mayer, Ji Mazak, the late Vratja Mazák, Erik Meijaard, the late Erna Mohr, Guy Musser, Gertrud Neumann-Denzau, William Oliver, Rohan Pethiyagoda, Francis Petter, Pierre Pfeffer, Roberto Portela Miguez, M. K. Ranjitsinh, Tom Roberts, Jan Robovsky, Kees Rookmaaker, Terri Roth, Klaus Rudloff, Maria Rutzmoser, Jaffar Shikari, Chris Smeenk, Kes Smith, Atanas Tchobanov, Dirk Thys van den Audenaerde, Louise Tomsett, Michel Tranier, Marc Vassart, Wang Sung, Wang Yingxiang, Eileen Westwig, Henning Wiesner, Detlef Willborn, Don Wilson, Roland Wirth, Derek Yalden, Yang Chan Man, Yang Qisen, Zainal-Zahari Zainuddin, Tatjana Zharkikh, and the late Klaus Zimmermann. Above all, we would like to thank Phyll and Eileen, who have been with us and supported us all the time.

WHAT ARE UNGULATES?

“Ungulate” means “having hoofs.” This is nowadays taken to imply that part of the terminal phalanx is encased in a sturdy hoof, although Lydekker (1913) required, inferentially, only that the toenail be thickened for it to count as a hoof; hence, his inclusion of elephants and hyraxes in his catalog of ungulates.

This book takes ungulates to be members of the Artiodactyla and Perissodactyla; moreover, not all of the Artiodactyla are ungulates, if the Cetacea should actually be included in the order (as they should be, to make the Artiodactyla monophyletic).

A NOTE ON SYNONYMY

The synonymies given for most of the taxa we list are incomplete. Given that full synonymy lists are readily available in other sources, we have thought it unnecessary to repeat them here. In general we include only those synonyms that are little known or controversial or otherwise contextual. Synonymy entries that we consider doubtful are preceded by a question mark.

IN MEMORIAM: PETER GRUBB

My friend and colleague Peter Grubb died in late December 2006 (Groves, 2006b).

We were first introduced by the late Peter Jewell in 1970, and we repaired to a pub in London to talk about our mutual interests. I knew that Peter had done fieldwork on Soay sheep on the island of Hirta in the Outer Hebrides, and on giant tortoises on Aldabra in the Indian Ocean, so at first I was slightly surprised that he was interested in mammalian taxonomy. It turned out that this was, in fact, a consuming passion for him, one that had overtaken animal behavior. We started to plan strategies, beginning with a research trip around European museums (Berlin, Bonn, Frankfurt, Leiden, Tervuren) in 1973, after which we separated to take up posts overseas, I in Canberra, he in Accra. From these distant centers we would write to each other, gradually work up papers together, and send each other our sole-authored manuscripts for comment. “Groves and Grubb” alternated with “Grubb and Groves” in the literature, and our colleagues got the impression that we were making a takeover bid for the ungulates, perhaps for all the mammals.

The unfortunate thing was that, while my post was a continuing one, and I happily established my teaching and research profile at the Australian National University, Peter’s, at the University of Ghana, was a fixed-term appointment. At its termination in the late 1970s, when he returned to the UK, he found a very tight market in the university world. Most zoology departments were not especially interested in taxonomy at the time; he did apply for an advertised post in animal behavior, and was shortlisted, but he was, in effect, not very interested and withdrew. And so it was that he became a schoolteacher.

He was not unhappy teaching biology, but chafed a little under the restrictions of the system. It meant that he had comparatively little time now for his research, but his friends supported him in his applications for leave to make overseas research trips—notably, a very productive one to museums in North America—and his output, plus our joint output, continued, only much more slowly than before. As his reputation grew, he came to be invited to more and more conferences and symposia, though I doubt whether his school ever really realized what a gem they had on their hands. His first and only trip to China, to take part in the cataloging of the rediscovered Heude collection (Braun et al., 2001), was shorter than planned, simply because his employers grumbled at the prospect of him staying away for more than two weeks.

Different professional colleagues will remember him for different things. In ungulate taxonomy, he will long be remembered as the person who replaced assumptions by research and wrote the first sensible things for half a century or more on such groups as African buffaloes (Grubb, 1972), bushbuck (Grubb, 1985a), or wild pigs (Grubb, 1993b); I myself got straightened out about musk-deer in a revealing paper (Grubb, 1982b). Wild pig aficionados think of his astonishing demonstration that warthogs are much, much more interesting than they had envisaged! Meanwhile, primatologists began increasingly to call on his expertise, such as at an important symposium on primate taxonomy in Orlando, Florida, in 2000.

He was always interested in the bigger picture: relationships between forest and savanna-living relatives in Africa, and interrelationships among African forest faunas. His papers on African forest biogeography are by now standard texts: patterns of speciation (Grubb, 1978a), rainforest biogeography (Grubb, 1979, 1982a, 1990b, 1999b, 2001b), and—throwing light on a neglected field—the East African forest biome (Grubb, 1985b). There is no doubt that his expertise, perspicacity, and insights will be greatly missed.

When, after his death from cancer, I finally began to organize a project that we had always had as a future ambition, a book on ungulate taxonomy, I was invited by his wife Eileen, and his old colleague Barry Hughes, to go through his papers. To my astonishment, there were manuscripts almost ready to be sent for publication, and acres and acres of notes and measurements that he had taken in museums over the years but never found time to work up into publishable form. Using his data, and incorporating his manuscripts (in different stages of completion), I decided to make this book the culmination of the "Groves and Grubb" series. My European research trip in 2009 was made thoroughly manageable by the knowledge that a lot of the basic work had already been done by Peter, and I had mainly to fill in gaps.

I will miss my old friend. I will miss our communications by letter and by e-mail, and, even more, I will miss our too-infrequent meetings, usually when I visited London. We would plan to spend some days together at the Natural History Museum, but our time would begin with sitting down together in an Indian restaurant, shaking hands or slapping palms, and at once beginning to talk as if we had never been apart.

Colin Groves

Theory of Ungulate Taxonomy

WHAT IS TAXONOMY?

It is still true that taxonomy is regarded to some extent as the poor relation of ecology and behavior, but it is again becoming more fashionable nowadays, riding, at least partly, on the coattails of the molecular revolution. The general public, too, are becoming more and more aware of biodiversity and get excited about the discovery or identification of new species; taxonomy, of course, is the basis for understanding biodiversity, as was recently emphasized by Cotterill & Foissner (2009) in the context of the importance of museum collections.

At its best, a taxonomic arrangement (above the species level) is a two-dimensional readout of phylogeny: taxa of the same rank are sister groups, and as the rank/time depth nexus becomes accepted, the level at which these sister groups are ranked tells us approximately when they separated in evolutionary time. This is not always possible: there are only so many taxonomic ranks to go around (not a problem if we want to junk ranks altogether and adopt the phylocode, of course—which we do not), splitting may not always be dichotomous, and we sometimes have evidence of past reticulations. Nonetheless, taken cautiously, a taxonomic scheme can perform something of this function.

SPECIES

In essence, a species is "a lineage . . . evolving separately from others and with its own evolutionary role and tendencies" (Simpson, 1961). This is true, in the sense that it says why species are important in the grand scheme of things (as the units of biodiversity), but it is not useful when it comes to actually identifying them and discriminating them from each other. We are in need of an operational definition. One of us has argued extensively (Groves, 2001a, b, 2004) that what is known as the Phylogenetic Species Concept (PSC) fills this need.

In this book, therefore, we define a species (in sexually reproducing organisms) as follows: "A species is the smallest population or aggregation of populations which has fixed heritable differences from other such populations or aggregations" (modified following Eldredge and Cracraft, 1980; Nixon & Wheeler, 1990; and Christofferson, 1995; also see Groves [2001a, b, and especially 2004] for discussions of the implications of this concept).

Note that, under the PSC, species have to be distinguished by fixed character states, but—in most versions of the concept—these character states do not have to be autapomorphic. It is perfectly feasible that, when a parent species splits into two, evolutionary changes may occur, and even accumulate, in just one of the daughter species, the other persisting essentially unchanged from the parent species; this, indeed, is the basis for progressive clines (see Grubb, 2000a).

We must admit that, when looking at the morphological or other phenotypic features (behavioral, ecological) that differentiate species, it is not always possible to demonstrate that the differences are heritable, but it is important to identify the units of biodiversity that are species, so we argue that it is advisable to start by acting as if they are, until it is shown otherwise.

The advantage of the PSC is that it depends entirely on the evidence to hand; there is no extrapolation.

The Biological Species Concept (BSC), which was the dominant concept of (sexually reproducing) species for some half century following on the great evolutionary synthesis of the 1930s, defined species as being "reproductively isolated," meaning that they did not interbreed with one another in a state of nature. Many biologists still use the BSC as their guiding principle, even if only lip service is paid to its primacy. There are, however, two glaring problems with the BSC, and either, by itself, would be sufficient to raise doubts about its universal applicability.

The first problem concerns allopatric populations, that is to say, populations that are completely out of contact with one another, because they are separated by barriers of some kind (water barriers, tracts of unsuitable habitat, mountain ranges). In such cases, the BSC obliges the taxonomist to hypothesize whether interbreeding "might" occur if their ranges were to meet. This results in an impossible situation: how would one know? The distributions of the black-faced impala and the common impala do not overlap; they have no possibility to interbreed in nature, so how should we classify them? Other criteria began to creep in: are they "different enough" to be ranked as distinct species, or not? In short, the BSC offers no guidance when it comes to allopatric populations, and we are reduced to untestable hypotheses. Don't get us wrong; the book by Mayr (1963), premised on the BSC, is a remarkable piece of work, and even today one can learn endlessly from it, but, over time, the species concept it promotes has been shown to have irreparable flaws.

The second problem is, quite simply, that it is wrong. What we have called the molecular revolution has shown that species actually do interbreed in nature; yet they nonetheless persist as discrete entities. Whitetail and mule deer are widely sympatric in North America and demonstrably form separate entities in nature, yet they often have each other's mitochondrial DNA (mtDNA)! Evidently they were intermittently interbreeding, undetected by biologists prior to the 1980s. We will say more about this below; but, for the moment, the important point is that to say that different species are "reproductively isolated" can often be shown to be incorrect.

Paterson (1978, 1980) proposed that a species has its own Mate Recognition System, and that this is the overriding criterion for species rank: what he termed the Recognition Species Concept. This puts us back into the realm of hypothesis, though in a rather different way from the BSC. In most living species, behavioral studies are simply not sufficiently advanced to be able to determine, with any degree of certainty, what these recognition features actually are; in the case of fossil species, one can never know. It is easier to have a "good guess" in the case of many ungulates than, for example, in primates or rodents, but that is all it is. There is an intense interest in detecting what sort of interactions seem to matter in a mating context, and how these patterns differ in various species, but one cannot use these observations as the basis for deciding whether they are actually separate species or not, even if one were certain that one did have complete information.

The Phylogenetic Species Concept does not depend on hypothesis, nor on extrapolation; it depends on the evidence to hand. If the evidence before us indicates that, in some character state or other, two operational taxonomic units (OTUs) are discrete (i.e., nonoverlapping), then the two OTUs are to be classified as distinct species. Further data may show that there is, in fact, overlap, so that the decision to class them as distinct species was wrong, but the important point is that the decision always depends on data, never on extrapolation or hypothesis. The only point at which we are forced to extrapolate is in the inference that the OTUs in question are different populations. Species must be populations in any species concept—there is no getting away from this inference, ever—and unfortunately this is just something that we have to live with; once we have made this extrapolation, we can get back to the dataset without making any more hypotheses. If this results in more—perhaps many more—species being recognized than previously, surely it is a small price to pay for exactitude?

This is as close as we can come to putting a finger on the units of biodiversity. The next level— where we start deducing how these different units are related to each other, what ecological roles they perform, and their relationship to geography—is where the excitement begins for many workers, and we can only agree that this is a matter of intense interest (see, for example, the geospecies concept in Grubb, 2006). Likewise, we have to ensure the conservation of these units, and, if there are more of them than we formerly thought, then more care, and probably more finances, will have to be involved. But first we have to determine what the units actually are.

The characteristics of species under the PSC are therefore as follows:

—They are the terminal points on a cladogram; that is, they are the least inclusive phylogenetic units.
—They are discrete units; that is, it is below the species level that relationships are reticulate (and yet some species are undoubtedly the products of hybridization!—see below).
—They are 100% diagnosable; that is, they have fixed heritable differences between them, though these may, in fact, be expressed only in one sex or at one stage in the life cycle.
—They are genetically isolated, though not necessarily reproductively isolated.

The criteria by which species may be recognized may be morphological, or perhaps physiological or behavioral, or they may be base-pair differences in a DNA sequence. We cannot privilege one source of information over another, as long as there is at least a presumption that they are heritable (to be tested, if feasible).

MOLECULES AND MORPHOLOGY

We have found, and recorded in this book, that in many cases the evidences from DNA (the "molecular evidence") and morphology, including morphometrics, are consilient: they give the same results. In other cases, however, they are inconsistent. In former days, when DNA sequencing was its infancy and was very like magic to most nonpractitioners, the demonstration that two hitherto established taxa were not much different in, say, the control region, was held to require that they should be synonymized: DNA was "the answer." We now know much better; we have remembered that phenotypes result from genotypes (plus, potentially, from an input from environmental effects), so these are also, in their own way, telling us about genetics.

There are several reasons why DNA data, especially mtDNA, might not send precisely the same message as morphology. First, we might have the persistence of ancestral polymorphism in DNA, particularly mtDNA, so that two given populations might not have achieved reciprocal monophyly. R. G. Harrison (1998) has calculated that, where N is the size of the two populations, and if N has remained approximately constant over time, then the probability of reciprocal monophyly in mtDNA sequences is about 35% after N generations, 57% after $2N$ generations, and 83% after $4N$ generations. Two daughter populations of 10,000 individuals each—not an inflated figure for many mammalian populations—will therefore need 20,000 generations to have an even chance of reciprocal monophyly; if an average artiodactyl generation can be envisaged as about five years, this translates to 100,000 years. On the other hand, reciprocal monophyly for a nuclear DNA (nDNA) sequence will be, on average, four times that for an mtDNA sequence and, as morphological characters result from nDNA (not from mtDNA), cases where a population will be homogeneous morphologically, but similar to its neighbors in mtDNA, will be uncommon for this reason, but not impossible.

This, however, applies only in the neutral evolution case. If selection is involved, all bets are off. Thus the second reason why DNA sequences and morphology may be offset is if there has been a selective sweep in one or the other. An example of this might be the case of the plains zebra, *Equus quagga*, in which—despite the clear geographical differences in morphology (striping, size, incisor cupping, mane)—there is no such structuring in mtDNA (Lorenzen et al., 2008b). Evidently, a fairly recent advantageous mutation occurred in the mitochondrial genome (remembering that mitochondrial genes code for important functions in metabolism) and moved rapidly through the species.

The third reason, of course, is introgression. Hybridization between two species is frequently asymmetrical. This idea was first put forth more than half a century ago by Flerov, who described hybrids between sika and wapiti in N China and the Russian Far East: "These hybrids are encountered comparatively frequently in the wild state and have long been known to the Chinese. The male wapiti during rutting drives away the weaker spotted deer male and covers his females" (Flerov, 1952:142 [126 of the English translation]). If this superiority of wapiti stags also applied over hybrid stags in F_1 and subsequent generations—as it well might, since the size of the hinds would increase in consecutive backcross generations, and they would become accessible only to wapiti stags—then the proportion of sika nDNA would halve in each successive generation, until we would we end up with populations that were effectively wapiti but with sika mtDNA. This effect, known as nuclear swamping, seems widespread among ruminants, as we will discuss in several places in this book.

SUBSPECIES

Subspecies are, in principle, geographic divisions of a species. There are strong differences in the frequencies of their particular character states, but subspecies are not absolutely different: they overlap. Therefore they are, to an extent, arbitrary and must in no case be reified.

In the past, there were too many subspecies: large numbers of subspecies are listed for most of the species in such key checklists as G. M. Allen (1939), Chasen (1940), Ellerman & Morrison Scott (1951), Hall & Kelson (1959), and Cabrera (1961). These subspecies may be differentiated into the Good, the Bad, and the Ugly.

The Good subspecies are 100% diagnosable; hence they are actually distinct species masquerading as mere subspecies—victims of the general feeling around the mid-20th century (and certainly under the influence of the BSC) that taxa should be, if possible, relegated to the status of subspecies of the nearest species as long as "they do not occur together" (a form of wording that constantly recurs throughout the checklist of Ellerman & Morrison Scott, 1951). As noted above, the BSC offers no guidance for the allocation of allopatric taxa, so that the classification of these taxa is forever unfalsifiable—it remains purely a matter of opinion.

The Bad subspecies are points along a cline, or are differentiated at very low frequency levels, or simply are based on one or two individuals that seemed outstanding at the time. The samples that they represent may be interesting for population genetics or in some other respect, but they have no taxonomic standing.

The Ugly subspecies are the ones which are left over. Subsequent studies have shown that they can be differentiated from other subspecies (i.e., from other geographic segments of the same species) at high frequencies, but they are not absolutely differentiated or diagnosable. The dilemma is, what to do with them? There does seem to be some advantage in dignifying them with a trinomial, especially for conservation purposes, but as these Ugly subspecies are arbitrary and unfalsifiable, one cannot insist upon it. Nonetheless, this is what we have in mind when we recognize subspecies in this book, unless we specifically state that they are "provisional,"

GENERA

Genera are monophyletic groupings of species. If a putative genus is shown to be nonmonophyletic, then it must be either be disbanded (by dividing it up into its monophyletic constituents), or expanded (by including in it the other putative genera whose independent existence rendered it nonmonophyletic in the first place), or narrowed (by taking out all but the nominotypical species and placing the former in the genera to which they are truly related).

Ropiquet & Hassanin (2005) found that the three species of the genus *Hemitragus* (known as tahr) were more closely related to other caprins than to each other: *H. jayakari* to the genus *Ammotragus*; *H. hylocrius* to *Ovis*; and *H. jemlahicus*, the nominotypical species, to *Capra*. They had three choices. First, they could keep all three species in *Hemitragus*, into which they would also sink *Ovis*, *Capra*, and *Ammotragus* (the prior available name would actually be either *Ovis* or *Capra*). Second, they could retain *Hemitragus*, but for *jemlahicus* alone, and place *jayakari* in *Ammotragus* and *hylocrius* in *Ovis*. Third, they could again retain *Hemitragus* to contain *jemlahicus* alone, but erect new genera for the other two species. They chose the third option (putting *jayakari* in a new genus *Arabitragus* and *hylocrius* in a new genus *Nilgiritragus*), but actually any of the three solutions is, under present circumstances, completely arbitrary.

It is surely abhorrent to maintain such an important taxonomic ranking, one whose name is the first word in a binomial, in this unfalsifiable limbo. Modifying previously expressed ideas going back to Willi Hennig half a century ago, Groves (2001a, 2004) argued that the genus category must be given some objectivity by linking it to time depth and suggested, by using the "principle of least violence," that this would be best put at about the Miocene–Pliocene boundary. Such time-depth information is not always—and even not usually—available, either from the fossil record or from the molecular clock; nonetheless, it is something to aim for, and future studies will doubtless modify some generic recognitions that we have used here.

As far as the tahr are concerned, Ropiquet & Hassanin (2005) gave the following mean separation times (under a local clock model): *Hemitragus* from *Capra*, 4.5 million years ago (Ma); *Arabitragus* from *Ammotragus*, 6 Ma; *Nilgiritragus* from *Ovis*, 4.5 Ma. Under the Groves regime, the genus *Arabitragus* would certainly be valid; the other two—including *Hemitragus* itself!—might be questionable. (Later, however, Ropiquet [2006:figure 18], in her preferred synthetic tree, put all these separations well into the Pliocene, in which case none of the genera could be maintained).

Groves (2001a, 2004) likewise argued that families, as well as genera, should have a time depth going back to the Oligocene–Miocene boundary.

In this book, no formal taxonomic conclusion should be drawn from the fact that, when a genus is large and relatively unwieldy in terms of the numbers of species it contains, we arrange the species according to *species-groups*. These are not intended to be monophyletic units, although they may be in many cases. Instead, they are simply grouping devices, the species within them being united on a phenetic basis.

The concept of geospecies, first used in ornithology, has been applied to primates by Grubb (2006), who defined the concept as follows: "Geospecies are lineages passing through an evolutionary history from the stage when they have lost allopatric sister taxa through extinction, to the stage when they have proliferated by cladogenesis, but not so far that daughter taxa have yet become sympatric." They are, thus, what have been called superspecies (monophyletic lineages of allopatric species), to which have been added species that stand on their own and do not belong to such diverse clusters. The problem with such concepts is always that they are rather fuzzy at the edges. Taxa may quite easily fail to be sympatric not because they have not diverged far enough, but because, however phylogenetically distinct they may be, they may be adapted to quite different ecosystems; or they may simply have retained their original ecological adaptations so as to exclude even distantly related taxa from sympatry. We do not here use the superspecies concept, preferring instead to use the phylogeny-neutral term species-groups, as explained above.

PHENOTYPIC PLASTICITY

In this book, one of the methods that we use a great deal is multivariate morphometrics, especially craniometrics. Geist (1989), however, has particularly urged that morphometrics is not a valid taxonomic tool, because of the ubiquity of phenotypic plasticity. In particular, he has cited the work of Franz Vogt who, in the 1930s, conducted experiments in red deer and roedeer breeding, rearing his unselected breeding groups on an especially high-quality diet (specifically, pressed sesame-seed cakes). Vogt found noticeable increases in body and antler size in both species, and these increases continued over four generations (presumably due to maternal effect); the differences were reversed in the red deer when they are were returned to less high-quality diets. The degree to which the conclusions from these experiments can be applied across the board, such as to the differences between "maintenance" and "dispersal" phenotypes, as Geist has propounded (both in his 1989 survey and elsewhere), is arguable, however. Deer, and also pigs, seem especially susceptible to the effects of different planes of nutrition and other factors (such as temperature) on growth, but these are much less evident in bovids, beyond some early effects, such as milk supply in single versus twin lambs (see the summaries in J. Hammond et al., 1983). In general, we take the "default" situation to be that wild animals, living in environments in which they can flourish and maintain viable populations, grow along a trajectory to achieve an adult size and shape where both are predictable from their genotype (within reasonably narrow limits). The argument maintaining that differences between two populations are entirely a result of environmental effects, or that environmental factors overwhelm genetic differences, needs to be substantiated.

MORPHOMETRICS

Both of us have taken substantial amounts of skull measurements (and sometimes collated flesh measurements) on most of the taxa treated in this book. We have worked out means, standard deviations, and absolute ranges for the measurements for geographic samples, or calculated one measurement as a percentage of another, or plotted two measurements together on a graph, or—whenever we could—included them in a multivariate analysis.

The ideal multivariate method is *discriminant analysis*. This is a method that requires specimens to be assigned to groups, and it then minimizes intragroup variation while maximizing intergroup variation. The major constraint is that there should not be too many variables (measurements, in this case) for the number of specimens per group: as a rule of thumb, most of the groups should have more specimens than there are variables, or we run the risk of a *type I error* (i.e., a false positive).

Sometimes discriminant analysis is not possible, and we use instead the rather unsatisfactory alternative of a *principal components analysis*, in which specimens are entered without grouping them. Whereas in discriminant analysis the different groups, whatever their size, are typically treated equally, so that small groups are given an equal chance to contribute to the final dispersion, in principal components analysis the less well-represented samples are "swallowed up" by the larger samples and fail to contribute equitably to the dispersion. Principal components analysis takes the raw measurements, which are all correlated with each other, and turns them into a number of independent variates; separating the input specimens into groupings is only incidental to the process, and groupings may not emerge at all. That is why, if at all possible, samples need to be grouped.

As long as sample sizes are large enough, the ideal is to compare different samples of restricted geographic origin with each other, aggregating those which turn out not to be discrete. Eventually, a picture is arrived at in which two or more of these aggregations may remain, and, if they are discrete and there is morphometric space between them, they then answer to the requirements of the PSC. If no discrete groups remain, then there is no morphometric evidence for different species.

In multivariate analysis, it is important that all the included measurements should be of the same kind, that is to say, either growth dependent or growth independent, and these two types of measurements should not be included simultaneously in the same analysis. *Growth-dependent measurements* are, in almost all of our cases, those of bone and/or horns. They increase with age, up to maturity at least (and beyond, in cases of indeterminate growth), and they bear an allometric relationship to each other. *Growth-independent measurements* are, in our cases, those of teeth. Teeth do not grow; they erupt and are then of a standard size (saving changes with wear, which usually means size reduction due to interproximal attrition), and they bear no allometric relationship with growth-dependent measurements. It may be of interest to make a bivariate plot between a measurement of skull size and a measurement of tooth size, but skull measurements and tooth measurements should on no account be combined in a multivariate analysis.

A BRIEF HISTORY OF THE TAXONOMY OF UNGULATES

Ungulate taxonomy has advanced, due to—or, in some cases, one might better say suffered under—a variety of sometimes colorful characters. Many of these also, of course, contributed to other areas in mammalogy, including primatology, and their accomplishments have been briefly recounted by Groves (2001a, 2008b), but a few of them will be further highlighted here.

Although Linnaeus (1758, 1766) described quite a few ungulates, the detailed description of species of ungulates did not really begin until the work of Pallas (1766, 1767–1777, 1811), who not only described new species on the basis of his travels throughout the Russian Empire, but gave scientific names to many others, based particularly on descriptions by Buffon, who had conscientiously refused to use Linnaean nomenclature. Pallas was followed, in particular, by Alfonse Desmarest (1822), who described new species from the growing collections of the Paris Museum (they had grown not only as a result of overseas collections by French explorers, but also by the activities of Étienne Geoffroy Saint-Hilaire and others who, as Napoleon conquered one country after another, had visited the museums and cabinets of the conquered countries and confiscated interesting specimens); and by Charles Hamilton Smith (1827), who likewise described many new species largely on the basis of the growing British Museum collections. Between them, these three authors described a surprisingly large proportion of the ungulate species that we recognize even today.

The British Museum collections continued to grow and were described by John Edward Gray—its assiduous, opinionated, and cranky mammal curator—who wrote catalog after catalog from the 1840s to 1870s (he died in 1873). In the 1830s and 1840s, the Museum's collections were enormously enriched by specimens sent by Brian Hodgson, first from Nepal and afterwards from a new base in Darjeeling. Unfortunately, his transfer from Nepal remained unremarked, so that many of these specimens, which were actually from Sikkim, Tibet, or elsewhere, have been labeled "Nepal," and it is only by looking at the date of acquisition and contextual information that these errors can be corrected. Hodgson himself described quite a large number of new species from Nepal, Sikkim, and Tibet; he also contributed his notes and color plates to the Museum's archives, and these are sometimes invaluable in filling in deficiencies of the collection (see, for example, Grubb, 1982b).

The latter half of the 19th century was an era of empire building by Western European nations; especially, this was the period of the notorious "scramble for Africa," which meant a further influx of large mammals—slain by explorers, empire builders, and the big game hunters who followed in their wake—into the British Museum (Natural History), which, by that time, had become a separate institution. These were described by Oldfield Thomas, Richard Lydekker, and others, with a growing contribution by Reginald Pocock who, after his retirement from the London Zoo (he took care to examine the animals that died there, particularly the ruminants, describing their skin glands, noses, and genitalia), worked on a voluntary basis at the Museum.

In France itself, mammalian taxonomy had almost dried up, but in Shanghai a French missionary, Pierre-Marie Heude, became passionately interested in natural history, especially large mammals, and was, whenever possible, diverting his attention from spreading the Word in favor of hunting, collecting live animals, and getting his brother missionaries and other colleagues to send him specimens—not only from China but from neighboring territories, which he loosely and inaccurately referred to as "the Chinese Empire": the Philippines, Indochina, Korea, the Russian Far East, and even Japan. He had not the least idea of species, and described hundreds of spurious ones—often half a dozen or more from exactly the same locality—in the midst of his few genuine ones. For a long time after his death (in 1905), his enormous collection remained underappreciated, and finally was lost to view, until it was rediscovered by CPG in 1996, and finally cataloged by us and our colleagues in 2000.

In the introduction to our catalog, we noted Heude's unchecked excesses of splitting and wrote: "Before we join in the near universal condemnation of this prolixity, it should be remembered that Heude stood at the threshold of a new era in mammalian taxonomy, when for the very first time large samples were becoming available. Used to samples of one or two specimens per region, from which one or two species would be described, the sudden embarrassment of riches proved overwhelming for many taxonomists. Heude was not the only one to suffer bemusement" (Braun et al., 2001:610), and we went on to instance C. Hart Merriam, the founder of American mammalogy, parts of whose record were at least as immoderate.

Despite these contributions, the period from about 1890 to 1924 was really the era of Paul Matschie. This extraordinary individual, perhaps the last notable holdout against the theory of evolution among professional zoologists, registered hundreds, even thousands of specimens, including (and especially) ungulates, that were sent to the Berlin Museum by explorers and hunters in the newly acquired German territories (which, in Africa, were Togo, Cameroon, Tanganyika ["German East Africa"], and Southwest Africa). He also paid regular visits to the Berlin Zoo and examined animals there. The result was an enormous profusion of new species and, when he came to adopt the concept, subspecies—and an overarching theory, outlined in his *Bemerkungen uber die Verbreitung der Tiere in den Deutschen Schutzgebieten* (Matschie, 1910a). For him, animal distributions were centered on river valleys; a rather sensible idea, one might say, but Matschie took it to extremes. Every major river valley had to have its own species in every species-group, and so did many rather minor ones; Matschie strove mightily to identify these species and the differences between them. The boundaries of their ranges were, of course, the watersheds between the river systems.

Every so often there would be an exhibition of game trophies in Berlin, and on most occasions Matschie would attend it and publish a report on it. His reports would be peppered with descriptions of the specimens in the exhibition, illustrated by photographs of mounted heads and horns in rows. Often enough, he would declare many of the trophies to represent new taxa (species and subspecies) and duly name them, even though the specimens concerned were mostly destined to disappear into the private collections of those who had obtained them; in a very few cases, the collectors would generously donate their specimens to the Berlin Museum, where at least they would be available in perpetuity, but mostly the only remaining evidence of these type specimens would be the small photos in Matschie's reports in the *Deutsche Jäger-Zeitung*.

Matschie also had a young admirer, Ludwig Zukowsky, who was, at that time, an assistant in the Berlin Zoo, but often came to study specimens in the Museum. In what may have been his first published paper (Zukowsky, 1910), he took Matschie's watershed idea to extremes. For example, apparently on the basis of conversations with Matschie (we cannot trace that Matschie had previously published the idea), hybrids between different species were to be identified by being asymmetrical. Again, in the light of modern work on hybrid developmental instability (Ackermann et al., 2006), this is not so unreasonable, but in Zukowsky's view it meant that the specific characters on one side were those of one of the parent species, and those on the other side, of the other parent species. Where should one expect hybrids? In watersheds, of course; and, in his notorious 1910 paper, Zukowsky identified some hybrids that he claimed came from watersheds. Famously, he figured the horns of a buffalo which had been shot in the district of Bihe, which he said was in the watershed of the N-flowing Cuanza and the SW-flowing Cunene and SE-flowing Cubango (= Okavango) rivers. Bihe, now called Kuito (although the province of which it is the capital is still called Bie [*sic*]), is at 12° 22' S, 16° 55' E, in a highland area that is indeed a watershed, although somewhat to the E of the sources of all the above-mentioned rivers. The horns in question are strikingly asymmetrical, the right horn being directed mainly forward and upward, left horn much more outward and backward. Zukowsky identified it as a hybrid between the Cunene and Cubango buffaloes, and mysteriously seemed to know which horn represented which buffalo, because he made the right horn the type of *Bubalus caffer cunenensis* (subsp. nov.) and the left horn the type of *Bubalus caffer cubangensis* (subsp. nov.) In the same paper, he did it again, describing *Bubalus caffer sankurrensis* and *Bubalus caffer lomamiensis* on another asymmetrical specimen, and *Bubalus rufuensis* on the left horn of a specimen of which he identified the right horn as belonging to the already-described *Bubalus schillingsi* Matschie. Matschie and Zukowsky later coauthored a series of three papers on Lichtenstein's hartebeest, which they divided into a large number of different species, again naming some of the new species on the evidence of one horn or the other of asymmetrical specimens (Matschie & Zukowsky, 1916, 1917, 1922).

Matschie got more and more mystical with age, substituting his watershed hypothesis with one called the "elementary areas of distribution," in which he divided the landscape into rectangles whose sides were the diagonals between every 2° of latitude and longitude (Matschie, 1920). In one of his last papers (Matschie, 1922), he described the distributions of what he regarded as three different species of kiang, thus: *E. kiang* 35/80, *E. holdereri* 37/100, and *E. tafeli* 35/99.

Matschie's colleagues continued to respect him for his vast knowledge, but had long since ceased to take him seriously as a taxonomist. And so it was that, in part as a reaction, mammalian taxonomy entered a world in which lumping held sway. The Phylogenetic Species Concept, proposed in 1983 (but foreshadowed in the 1970s), took a long while to enter mammalogy, although in retrospect its logic should have been more obvious; indeed, to a degree it is a return to the tacit species concepts of Oldfield Thomas and Gerritt Miller. Although one of us (CPG) was feeling his way toward this concept in the late 1990s, and finally published a book employing it (Groves, 2001a), it was only later that Peter Grubb (PG), after discussions with CPG and after reading the work of Cotterill (2003, 2005), also accepted the value of it. Nonetheless, PG decided to be conservative in his approach to species listing; in his contributions to Wilson & Reeder (Grubb, 2005a, b), he took the position that he ought to follow a policy of adopting the classification from the latest revision in each case.

DOMESTICATION

Many species of ungulates have been domesticated, and the evidence tends to suggest that in many cases what we view as modern domestic "species" are a mixture of several different domestication events, or at least a mixture to which several different wild populations have contributed. Some of what has been proposed on this score may, however, be spurious, if the conclusions of Ho et al. (2005) are justified, since these authors argued that rates of molecular evolution are initially extremely high, and then slow down after 1 million years or so. Molecular-clock calculations of the separation time between two domestic breeds often go back well into the Pleistocene, implying that the ancestors of the breeds in question separated well before actual domestication, so that they must be descended from different wild ancestors. If the Ho et al. model holds, however, then such early dates will need to be drastically reduced, and multiple domestication models may not always be necessary.

The nomenclature of domestic "species" has been problematic. After long literature discussions, going back at least to Bohlken (1958), the International Commission on Zoological Nomenclature (ICZN) finally made a ruling (ICZN, Opinion 2027, 2003). A. Gentry et al. (2004) explained what this means for the nomenclature of domestic animals: the name given to wild populations of species take precedence over those given to domesticates. Nonetheless, it is often convenient to continue to refer to domestic animals by their own scientific names, regardless of whether they might, in fact, be of mixed (hybrid) origin.

The first paragraph of the ruling states that under the plenary power, "it is hereby ruled that the name for each of the wild species listed in (2) and (3) below is not invalidated by virtue of being pre-dated by a name based on a domestic form" (ICZN, Opinion 2027, 2003:81). The names in question are listed in a further paragraph. Reference to this ICZN Opinion is made throughout this book in the appropriate places. The Opinion ends with the following sentence: "The names listed in the ruling above, which are the first available names in use based on wild populations, apply to wild species and include those for their domestic derivatives if these are not distinguishable."

PG always regretted that, under pressure of time, he at first did not appreciate the full meaning of the Opinion, and continued to use the names given to domestic animals for their wild ancestors in his contributions to Wilson & Reeder (Grubb 2005a, b). It is most unfortunate that this two-volume book was commissioned by the Smithsonian Institution Press, who then suddenly ceased publishing, and major changes were not permitted in the interim as new publishers for the photo-ready manuscript were sought. Hence the work, as finally published (by the Johns Hopkins University Press), was perforce not quite up-to-date—including in its treatment of domesticated species and their wild forebears.

The process of domestication is complex, but in each case it has apparently followed along somewhat parallel lines. For the biology of domestication, and brain-size changes in particular, see especially Hemmer (1983) and Kruska (2005, 2007).

In this book, we have decided not to deal with domestic animals in any depth. For completeness' sake, however, here is a list of the scientific names applicable to domestic species, together with their probable wild ancestors:

Equus caballus Linnaeus, 1758, horse—from *Equus ferus* Boddaert, 1785
Equus asinus Linnaeus, 1758, donkey (ass, burro)—from *Equus africanus* von Heuglin & Fitzinger, 1866
Camelus bactrianus Linnaeus, 1758, Bactrian camel—from *Camelus ferus* Przewalski, 1878
Camelus dromedarius Linnaeus, 1758, Arabian camel (dromedary)—wild ancestor unknown
Lama glama (Linnaeus, 1758), llama—from *Lama guanicoe* (Müller, 1776)

Lama pacos (Linnaeus, 1758), alpaca—from *Lama guanicoe* (Müller, 1776) × *L. vicugna* (Molina, 1782)

Sus domesticus Erxleben, 1777, pig—from *Sus scrofa* Linnaeus, 1758, and other species

Bos taurus Linnaeus, 1758, European (humpless) cattle—from *Bos primigenius* Bojanus, 1827

Bos indicus Linnaeus, 1758, humped cattle (zebu)—from *Bos namadicus* Falconer, 1859

Bos frontalis Lambert, 1804, mithan—from *Bos gaurus* Hamilton Smith, 1827

Bos javanicus domesticus Gans, 1916, Bali cattle—from *Bos javanicus* d'Alton, 1823

Bos grunniens Linnaeus, 1766, yak—from *Bos mutus* (Przewalski, 1883)

Bubalus bubalis (Linnaeus, 1758), water buffalo—from *Bubalus arnee* (Kerr, 1792)

Capra hircus Linnaeus, 1758, goat—from *Capra aegagrus* Erxleben, 1777

Ovis aries Linnaeus, 1758, sheep—from *Ovis gmelini* Blyth, 1841

CONSERVATION

We unfortunately live in a time when the preservation of the world's biodiversity is in crisis. While we may only infer that substantial numbers of invertebrates are going extinct, unremarked, every year as their habitats disappear, ungulates are large and visible, and the continuing drastic declines in their numbers and ranges are all too obvious. We have said little about this under the different species' headings, but, as one of the major aims of this book is to document taxonomic diversity, we must draw attention to it here. Species treated in this book that are in imminent danger of extinction are listed below. We do not list subspecies, though some, like *Hippotragus niger variani*, are also highly endangered in their own right. We have selected only the most critically endangered:

Equus przewalskii—persists only in captivity, although most of the captive stock consists of what is called the B-line, known to be partly descended from at least two domestic horses; the A-line, almost certainly descended from pure-blooded Przewalski horses, numbers somewhat over a hundred individuals.

Equus africanus—the nominotypical subspecies is possibly extinct, though it may persist as a captive stock (possibly from the hybrid zone?) in private hands; subsp. *somaliensis*, perhaps a distinct species, is critically endangered in Somalia, but a few hundred are protected in Eritrea.

Rhinoceros unicornis—slowly increasing in number under protection.

Rhinoceros sondaicus—the second-rarest of all large mammals, only ±60 remain, but protected.

Dicerorhinus sumatrensis—only 200–300 remain, not well protected.

Diceros bicornis—in the 1970s and 1980s, suffered the most astonishing crash in numbers known for any large mammal, from nearly 100,000 to only 2500 individuals; now very slowly increasing under protection.

Ceratotherium cottoni—on the verge of extinction, only 10 known to survive, all in captivity or semicaptivity.

Choeropsis heslopi—not reported since 1943.

Dama mesopotamica—very low numbers in the wild; bred in captivity.

Rucervus schomburgki—presumed extinct since the 1930s.

Panolia (all species)—persist only in very small populations, except for those on Hainan Island; *P. eldii* from Manipur, whose numbers were once as low as 14, has, however, increased to more than 200 under protection.

Cervus pseudaxis—number unknown in the wild, but the amount is certainly very small; bred in captivity.

Cervus alfredi—number unknown in the wild, but the amount must be extremely small; bred in captivity.

Bos sauveli—probably extinct, but searches for it continue.

Bubalus arnee—survives only in small isolates.

Bubalus mindorensis—perhaps 200–300 survive.

Pseudoryx nghetinhensis—still illegally hunted, despite its small numbers; restricted range and nominal protection.

Gazella acaciae—only about 20 remain; now protected.

Gazella arabica—not seen since its original description, 180 years ago.

Gazella bilkis—may be extinct, or nearly so, because of overhunting.

Eudorcas rufina—not recorded since the 1880s, and presumed extinct.

Procapra przewalskii—only about 200 remain, in small isolated populations around Qinghai Lake and on the Buha River.

Alcelaphus tora—uncertain whether any still exist.
Beatragus hunteri—500–1000 remaining; declining in its original habitat; introduced into Tsavo East National Park, where about 100 persist.
Damaliscus selousi—unknown if any still exist.
Oryx dammah—extinct in the wild, though breeding well in captivity.
Oryx leucoryx—well represented in captivity, but populations reintroduced into the wild have been under constant threat from poaching.
Addax nasomaculatus—reduced to a few small, fragmentary populations.
Capra walie—found in small fragments, mainly in Semyen National Park, Ethiopia, where it has recently increased to about 500 under protection.
Cephalophus jentinki—threatened by hunting and habitat loss in its very small range.
Cephalophus adersi—survives in only very small numbers in both known populations (Zanzibar, and Sokoke Forest in Kenya).

BIOGEOGRAPHY OF UNGULATES

The pictures of the biogeography of ungulates that emerge from this book will take some time to analyze and digest, but we would like to draw attention to a few findings, some of which were unanticipated:

—Vrba's stenotypic versus eurytopic division—This, which in hindsight now seems so obvious, is abundantly confirmed. We return to this theme in our introduction to the Bovidae.
—The Sudanic grasslands ecosystem—Many species are spread throughout this ecosystem, from Senegal in the W to the borders of Ethiopia in the E, with little or no geographic variation, except sometimes for minor differentiation W and E of the Nile. This contrasts with many of the same species-groups in E and S Africa, where their ranges are restricted to isolates. An example would be the contrast in the *Damaliscus korrigum* group between the Sudanic *D. korrigum* (with the dubiously distinct *D. tiang* E of the Nile) and the five species dotted around the E African landscape.
—The Serengeti-Mara ecosystem—It contains a number of apparently unique species. It is therefore important not only as an example of a nearly intact E African ecosystem in its own right, but also as the sole repository of a range of endemic species.
—The lower Oubangui River—Wide as it is, this river appears to be insignificant as a faunal barrier; many forest species (in ungulates as in primates) go right across it as if it did not exist. There is some suggestion that its upper course, mostly a continuation of its major constituent, the Uele River, was at one time (during the Early Holocene?) part of the Shari-Logone system, and has since been captured by the Congo to form the lower Oubangui.
—The Cape region—It has its own range of species, separate from their congenerics farther N.
—Lower Yangtze River—There is a special ecosystem S of the lower Yangtze, apparently centered on Lake Po-yang, with its own species (as far as ungulates are concerned) of deer and pigs.
—Russian Far East—Finally, we would like to draw attention yet again, as has been done previously (especially in Russian works), to the separate faunal status of the Russian Far East, including at least parts of the Korean peninsula and the Manchurian provinces of China.

ORGANIZATION OF THE TAXONOMIC SECTIONS

In each case, after introducing the family, we discuss its constituent genera in turn, listing species (and subspecies, where applicable) either before or after we have detailed our own research and/or that of others. As noted in the introduction, we have not invariably listed complete synonymies.

PART I: PERISSODACTYLA

THERE ARE NO particular problems in the order Perissodactyla, at least at the higher levels: there are three families in the living fauna, and, as far as we know, no one has demurred from this assessment.

All perissodactyls are hindgut fermenters; none has a complex stomach, and all have a large caecum and colon.

From being the most diverse ungulates in the Oligocene, they began to decline in the Miocene, presumably in the face of competition from the rising artiodactyls, and today perissodactyls are greatly reduced in both diversity and abundance.

3

Rhinocerotidae

RHINOCEROTIDAE GRAY, 1821

The most up-to-date survey of the status of living rhinos is by Amin et al. (2006). On rhinoceros taxonomy and evolution, see Groves (1997c).

It was Flower (1876) who laid the basis of modern rhinoceros taxonomy by reducing the number of recognized species to a provisional six (one of them regarded as extremely doubtful) and arranging them into three genera. Flower also listed and described the most cogent characters by which the species can be recognized, illustrating some of them. Groves (1971) elucidated the differences between the horns of the existing taxa.

There have been many attempts to decipher the exact branching order of the three major lineages: *Rhinoceros*, *Dicerorhinus*, and African rhinos (*Diceros* and *Ceratotherium* being universally accepted to be branches of the same major lineage). Groves (1983a), for example, on the basis of a detailed survey of skulls and teeth, put *Dicerorhinus* closer to *Rhinoceros*. The latest attempt (Willerslev et al., 2009) was unable to resolve the pattern: the separation times, regardless of whether *Rhinoceros*, *Dicerorhinus*, or the African lineage separated first, were all between 32 and 30.4 Ma (note that a mean of 60 Ma was specified for the age of the root [i.e., separation from other perissodactyls], and used as the calibration point—which some paleontologists might think outrageously early!).

Rhinoceros Linnaeus, 1758

A single pair of large, compressed, blocklike upper incisors, with (at least in the young adults) a much smaller lateral pair; mandibular central incisors very small, the laterals large, procumbent, and pointed, forming formidable tusks. Postglenoid and posttympanic processes united below the external auditory meatus. Occipital plane very wide, forming a flat-topped triangle in posterior view, and sloping forward in lateral view. Dorsal outline of the cranium deeply concave. Foramen magnum more or less triangular. Nasal bones anteriorly pointed. (Following Flower, 1876; Pocock, 1945; Chakraborty, 1972.) Externally, there are deep folds in the skin, as follows: along the angle of the jaw (much deeper in the males than in the females); two to three vertically around the neck, with one emerging posteriorly and running horizontally for some distance, about halfway up the thickness of the neck; vertically anterior to the foreleg; horizontally around the base of each foreleg; vertically posterior to the foreleg, travelling across behind the shoulder to meet its opposite number on the other side; vertically anterior to the hindleg, crossing in front of the croup to meet its opposite number, and continuous, with one going horizontally across the base of each hindleg; posterior to each hindleg, going vertically across behind the croup and above the tail; and, finally, one running horizontally from the posterior hindleg fold, level with lower surface of the tail base, and usually not reaching the anterior hindleg fold. Body hairs sparse, but locally detectable in certain lights and to the touch. One single nasal horn.

A survey of the Asian rhinos, incorporating much of what was known up to that date, is in Groves (1982a).

Rhinoceros unicornis Linnaeus, 1758

Indian one-horned rhinoceros, greater one-horned rhinoceros

1758 *Rhinoceros unicornis* Linnaeus. Rookmaaker (1998) showed that the sources for this species actually included *R. sondaicus*, as well. The lectotype is the rhino in Dürer's famous woodcut of 1515.
1779 *Rhinoceros rugosus* Blumenbach. For this name, see Rookmaaker (2004).
1875 *Rhinoceros jamrachi* Jamrach. Manipur.
1970 *Rhinoceros unicornis bengalensis* Kourist. Bengal.
Only synonyms not listed in Ellerman & Morrison Scott (1951) are given here.

In the upper molars and premolars, the crochet and the crista become united with wear, cutting off an accessory valley from the medisinus. The posterior end of the vomer is thickened, fused to pterygoid plates on either side; the mesopterygoid fossa is narrow, the bases of the pterygoid plates almost meet posteriorly.

The skinfolds are deep, and hang loosely; the horizontal fold emerging posteriorly from the neck folds is short, petering out before reaching posterior foreleg fold. The body skin is studied with low knobs. Sexual dimorphism in the development of the mandibular and neck folds is considerable: adult males develop a noticeable "bib."

The upper lip has a short median point, which is used for browsing, but more usually the point is "tucked in," so that the lip becomes a wide cropping organ.

Rookmaaker (1980) has traced the recent distribution of this species, at least as far as India, Bangladesh, and the Indochinese region are concerned. It was known in modern times from Bihar E through N Bengal and Assam, perhaps just entering Bangladesh, as far E as the Tirap Frontier tract (uncertain), and possibly even into N Laos.

Rhinoceros sondaicus Desmarest, 1822

Javan one-horned rhinoceros, lesser one-horned rhinoceros

The upper molar and premolar crochet and crista almost never fuse.

The posterior end of vomer is thin, free from pterygoids; the mesopterygoid fossa is wide. (Mainly following Flower, 1876; Pocock, 1945.)

The skinfolds are much "tighter" than in *R. unicornis*; the horizontal fold emerging posteriorly from the neck folds slants upward, crossing the withers to join its opposite number on the other side, forming a kind of "saddle" about it. The skin has no raised knobs, but it is covered by a network of very fine cracks; the head is small in proportion to the bulk of the body; the females are slightly larger than the males, on average, and the males develop only a small "bib."

The upper lip is long and pointed, suitable for browsing; the premaxilla does not fuse to the maxilla until old age, extending the gape and increasing the mobility of the upper lip.

The horn in the male is smaller, and more slender, than in *R. unicornis*, and the supporting nasal bones are narrow; in the females, the horn is very reduced.

The characterizations of the subspecies follow Groves (1967a), and especially Groves & Guérin (1980); see also Groves & Chakraborty (1983). Some of the differences appear discrete, and nonoverlapping, and the Indochinese and Bengal taxa are theoretically candidates for recognition as full species, but caution is required, since only very small sample sizes are available.

Rhinoceros sondaicus sondaicus Desmarest, 1822

1822 *Rhinoceros sondaicus* Desmarest. Java; exact locality indeterminable (Rookmaaker, 1982).
1824 *Rhinoceros javanicus* E. Geoffroy & F. Cuvier. Java.
1827 *Rhinoceros camperis* Griffith. Java.
1829 *Rhinoceros javanus* G. Cuvier. Java.
1836 *Rhinoceros camperii* Jardine. Java.
1868 *Rhinoceros floweri* Gray. Sumatra.
1868 *Rhinoceros nasalis* Gray. "Borneo," probably Java.
1876 *Rhinoceros frontalis* von Martens. Error for *Rhinoceros nasalis*.
The full synonymy is given here, following Rookmaaker (1983).

Dentition relatively small; palatine bones 44%–53% of the total palate length (posterior to the incisive foramina); palatine bones >80% as wide as long, and usually longer; mandibular corpus not greatly deepening posteriorly, its depth at the third molar 111%–144% of that at the second premolar; on P^2, protoloph fusing with the ectoloph with wear; anterior premolars (probably actually milk molars) remaining in place for much of the animal's adult life; crochet on the premolars usually doubled; crista on the premolars usually much reduced on Sumatran and mainland individuals, but often quite absent on those from Java, and absent on the molars in all animals.

Java, Sumatra, and the Malay peninsula as far N as Tenasserim. Survives, as far as is known, only in Ujung Kulon National Park, westernmost Java.

Rhinoceros sondaicus annamiticus Heude, 1892

1892 *Rhinoceros annamiticus* Heude. Tay-ninh, 700 km from Saigon (see Braun et al., 2001).
Rookmaaker (1983) gave the corrected reference to this name.

Nuchal surface more inclined anteriorly; facial skeleton relatively low, with a comparatively deep dorsal concavity; palatine bones 39%–63% of the total palate length; palatine bones 36%–66% as wide as long; mandibular body as in nominotypical *R. s. sondaicus*; in P^2, protoloph fusing with the ectoloph with wear, as in nominotypical *R. s. sondaicus*; anterior premolars (probably actually milk molars) remaining in place for much of the animal's adult life; crochet on the premolars usually not doubled; crista usually absent on the premolars, but usually present, though small, on the molars. Long bones apparently longer and more slender than in nominotypical *R. s. sondaicus*; medium metapodials shorter and wider.

Rookmaaker (1980) noted that this subspecies is depicted on a relief in Angkor Wat in Cambodia and he gives evidence that it may still have existed in S Laos at the time of his writing. It possibly still occurs in Cat Tien National Park, NE of Saigon.

Rhinoceros sondaicus inermis Lesson, 1838

1838 *Rhinoceros inermis* Lesson. Sunderbans.

Dentition relatively large; palatine bones occupying a much larger proportion of the hard palate, >80% of the total palate length posterior to the incisive foramina; palatine bones 50%–80% as wide as long; mandibular corpus noticeably deepening posteriorly, its height at the third molar 167% of that at the second premolar; on P^2, protoloph remaining separate from the ectoloph, apparently throughout life; anterior premolars (probably actually milk molars) shedding before maturity; crochet on the premolars usually not doubled; crista present on the premolars, absent from the molars.

In females, the horn appears to have been absent altogether.

Now extinct. Rookmaaker (1980) has recorded its former distribution in India. *R. s. inermis* was known from Moraghat in the Bhutan Duars, probably the Sikkim Terai, the Sundarbans (where its more detailed distribution was given by Rookmaaker, 1997), and Chittagong. In Bangladesh, there is a record from Sylhet.

Dicerorhinus Gloger, 1841

The maxillary incisors are as in *Rhinoceros*; the mandibular central incisors are lacking, but the laterals are tusklike. There is no subaural closure. The occipital plane is narrow, somewhat rectangular in posterior view, and more or less vertical in lateral view. The dorsal outline of the cranium is not strongly concave, with a slight convexity on the frontals. The foramen magnum is pear-shaped, its dorsal rim reduced upward into a narrow prolongation. The nasal bones are anteriorly pointed. (Following Flower, 1876; Pocock, 1945; Chakraborty, 1972.)

A survey of the Asian rhinos, incorporating much of what was known up to that date, is in Groves (1982a).

Dicerorhinus sumatrensis Fischer, 1814

Sumatran rhinoceros

The name *Rhinoceros crossii* Gray, 1854, belongs to this species, but to which subspecies is unknown.

On this species in general, see Groves (1982a). A survey of the biology of *D. sumatrensis*, intensively studied at the Melaka Zoo, has been given by Zainuddin et al. (1990).

The skinfolds are tighter than in *Rhinoceros*, and only the fold behind the foreleg travels over the shoulder to join the one on the opposite side. There are two horns, with the frontal horn placed well behind the nasal horn; the bases are not continuous. The skin of the nose is heavily cornified, lacking the wrinkles anterior to the nostril characteristic of other rhinos, with only a single deep crease running between the anterior margins of the nostrils from side to side, allowing mobility for the upper lip.

Body hair is comparatively long and profuse, compared with other rhinos.

A population aggregation analysis of mtDNA by Amato et al. (1995), using six individuals from Sumatra, four from Borneo, and seven from West Malaysia, found extremely low diversity: only a single haplotype on Borneo, one on the mainland, and two in Sumatra. Two variable sites differentiated the Borneo samples from the samples from Sumatra plus the mainland.

Subspecies follow Groves (1967a); see also Groves & Chakraborty (1983).

Dicerorhinus sumatrensis sumatrensis (Fischer, 1814)

1814 *Rhinoceros sumatrensis* Fischer. Fort Marlborough, Bintuhan district, Sumatra.
1822 *Rhinoceros sumatranus* Raffles. Sumatra.
1873 *Ceratorhinus blythii* Gray. Pegu.
1873 *Ceratorhinus niger* Gray. Sunghi-Njong district, Malacca.
1874 *Rhinoceros malayanus* Newman, nom. nud.
The full synonymy is given here, following Rookmaaker (1983).

Size large; teeth medium to small; occiput low, narrow.

Sumatra and the Malay peninsula, N to Pegu. The only certain records referable to it in the Indochinese district seem to be Nong Het (Laos), and Lao-Dao and Nhatrang (Vietnam), but whether they were referable to this subspecies is unknown.

Dicerorhinus sumatrensis harrissoni (Groves, 1965)

1912 *Rhinoceros borniensis* Hose & McDougall, nom. nud.
1965 *Didermocerus sumatrensis harrissoni* Groves. Suan-Lambah, Sabah.

Size small; teeth small; occiput narrow, but proportionally high, and forwardly inclined.

Borneo.

Dicerorhinus sumatrensis lasiotis (Sclater, 1872)

1872 *Rhinoceros lasiotis* Sclater. About 16 hours (as the elephant marches) S of Chittagong (Harper, 1940).

Size very large; teeth proportionately very large; occiput broad and high.

The northernmost subspecies, now perhaps extinct. The westernmost locality was the Sankosh River, and Rookmaaker (1980) mapped other records in India and Bangladesh.

Diceros Gray, 1821

The incisors are rudimentary (possibly only deciduous) or absent, and the front of both jaws is abbreviated. There is no subaural closure. The occipital plane is narrow, extending backward in lateral view, and overhanging the occipital condyles posteriorly. The nasal bones are much thickened, and truncated anteriorly. There are two horns, with the frontal horn placed immediately behind the nasal horn; the bases of the two horns are sometimes continuous. The upper lip is long, pointed, and mobile. Body hairs are lacking, except on a few specific places (the tail tip, the ear rims, and the base of the horns).

Diceros bicornis (Linnaeus, 1758)

black rhinoceros

The basic outlines of our knowledge of geographic variation were summarized by Groves (1967b) and Rookmaaker & Groves (1978). Rookmaaker (1995) proposed that this taxonomy, with later published amendments, should be used pending future work; he registered a strong objection to the practice, at that time becoming increasingly common, of using subspecific names for what authors specifically stated were "ecotypes." Later (Rookmaaker, 2005), he also deplored the tendency to "redefine the subspecies of the black rhinoceros on an ad hoc or geographically limited basis," insisting that they must be allocated with reference to real data.

Rookmaaker (1983) showed that the names *Atelodus bicornis* var. *plesioceros* and *A. b. platyceros* Brandt, 1878, belong to this species, but to which subspecies is not known; he showed however, that the name *A. b. porrhoceros*, occurring in the same publication, referred to an animal from Upper Nubia; hence, it is a synonym of *D. b. brucii*.

Harley et al. (2005) showed that, in the main, genetic differentiation in microsatellites between the subspecies was reasonably good, and that all individuals examined could be ascribed to their own subspecies with some confidence, with the exception of *D. b. chobiensis*.

Diceros bicornis bicornis (Linnaeus, 1758)

1758 *Rhinoceros bicornis* Linnaeus. As shown by Rookmaaker (1998), Linnaeus based this name on specimens both of this species and of *Dicerorhinus sumatrensis*. A neotype, with the locality being the Cape of Good Hope, was validly designated by Zukowsky (1965).

1797 *Rhinoceros africanus* Blumenbach.

1836 *Rhinoceros keitloa* A. Smith. Mafeking.

1842 *Rhinoceros gordoni* Lesson. Near the sources of the Gamka River.

1845 *Rhinoceros camperi* Schinz; not Jardine, 1836. Cape of Good Hope.

1845 *Rhinoceros niger* Schinz. Tsondap, Nuuibeb Mountains, S Namibia.

As before, the full synonymy is given here, following Rookmaaker (1983), who investigated the basis of the names given.

Very large in size, with large teeth. Mandibular first premolar apparently always absent in the adults. Maxillary [second, third, and fourth] premolars commonly possessing a crista. Radius under 80% of the humerus length (in all other subspecies, it is over 80%). Foreleg slightly shorter than the hindleg; limbs apparently rather slender. Skin apparently smooth, not deeply folded.

Formerly from the Cape N to Kuruman, and apparently to S Namibia, but not the coastal strip E of the Drakensberg. This subspecies has long been extinct; this vital information was inadvertently absent from Groves (1967b), but was emphasized by Rookmaaker & Groves (1978) in their general review of this subspecies. Unfortunately, the failure by Groves (1967b) to note that it was extinct has resulted in the name becoming (spuriously) widespread among wildlife workers for the still-extant Namibian population.

Diceros bicornis chobiensis Zukowsky, 1965

1965 *Diceros bicornis angolensis* Zukowsky. Virui waterhole, Mossamedes, Angola.

1965 *Diceros bicornis chobiensis* Zukowsky. Konsumbia, parent streams of the Loma River, tributary of the Cuando River, SE Angola.

Somewhat smaller than nominotypical *D. b. bicornis*. No crista on the upper premolars, or very minute. Skin with deep body folds.

Okavango region.

Apparently only a single individual is known to survive. This individual was studied by Harley et al.

(2005), using microsatellites; it was not well differentiated from *D. b. minor.*

Diceros bicornis minor (Drummond, 1876)

1876 *Rhinoceros bicornis major* Drummond. Country SE of Zambezi.
1876 *Rhinoceros bicornis minor* Drummond. Zululand.
1893 *Rhinoceros bicornis holmwoodi* Sclater. Udulia, 50 mi. S of Speke Gulf.
1947 *Diceros bicornis punyana* Potter. Hluhluwe.
1965 *Diceros bicornis nyasae* Zukowsky; a conditional name, hence unavailable. N end of Lake Malawi.
1965 *Diceros bicornis rowumae* Zukowsky; a conditional name, hence unavailable. Inland from Mikindani, Tanzania.
1972 *Rhinoceros kulumane* Player.

Still smaller in size. Externally, characterized by a short, compact body, with well- marked skinfolds and a large head. Mandibular first premolar apparently always absent in the adults in E Africa, but retained in 60% of those from Hluhluwe. No crista on the upper premolars, or very minute. Foreleg slightly longer than the hindleg.

From KwaZulu-Natal N into NW Tanzania and the SW borders of Kenya.

Diceros bicornis occidentalis (Zukowsky, 1922)

1922 *Opsiceros occidentalis* Zukowsky. Kaokoveld-Cunene region.

Size similar to *D. b. minor*; much broader across the zygomata. External phenotype resembling *D. b. chobiensis* and *D. b. minor.* No crista on the upper premolars, or very minute.

N Namibia and S Angola.

This subspecies was not recognized by Groves (1967b), but the study of a few more specimens has shown that it can be largely distinguished from *D. b. minor.*

Harley et al. (2005) studied microsatellites from 53 individuals of this subspecies (but unfortunately used the designation *"D. b. bicornis,"* for the reasons given above) from Namibia, and from populations reintroduced into South Africa. They were clearly assignable to their own subspecies, rather than to any other.

Diceros bicornis michaeli Zukowsky, 1965

1965 *Diceros bicornis michaeli* Zukowsky. Between Engaruka and Serengeti.
1965 *Diceros bicornis rendilis* Zukowsky. N Guaso Nyiro.

Still smaller (one of the smallest subspecies); relatively broad-skulled. External habitus the same as in *D. b. chobiensis*, *D. b. minor*, and *D. b. occidentalis*. Mandibular first premolar apparently always absent in the adults. No crista on the upper premolars, or very minute. Foreleg slightly longer than the hindleg.

NW Tanzania into E Kenya, including Tsavo and the N Guaso Nyiro.

Individuals of this subspecies studied by Harley et al. (2005) were differentiated, in microsatellites, from those of other subspecies he studied.

Diceros bicornis brucii (Lesson, 1842)

1842 *Rhinoceros brucii* Lesson. Tscherkin, between the Bahr Salaam and Atbara rivers.
1878 *Atelodus bicornis* var. *porrhoceros* Brandt.
1897 *Rhinoceros bicornis somaliensis* Potocki. "Somaliland."
? 1947 *Diceros bicornis palustris* Benzon. Near Aweng, N of the Lol River, Bahr-el-Ghazal.
1965 *Diceros bicornis atbarensis* Zukowsky. Anseba Valley, Eritrea.

Size as in *D. b. minor*; very narrow across the zygomata. Mandibular first premolar retained in the adults. Crochet on the maxillary premolars simple, not bifid (unlike most subspecies); these premolars commonly possessing a crista. External appearance, as documented in photographs, clearly different from those of *D. b. minor*, *D. b. occidentalis*, and *D. b. michaeli*, with the skinfolds much less marked.

Somalia, the Ogaden and N Ethiopia, Eritrea, and N Sudan E of the Nile; an isolated population, possibly attributable to this taxon, occurred in a small district of Bahr-el-Ghazal. Probably extinct.

Diceros bicornis ladoensis Groves, 1967

1965 *Diceros bicornis ladoensis* Zukowsky; a conditional name, hence unavailable under Zukowsky's authorship. Shambe, near Lado, southernmost Sudan.
1967 *Diceros bicornis ladoensis* Groves.

Larger than *D. b. minor*; broad-skulled, especially across the occipital crest. Mandibular first premolar apparently always absent in the adults. No crista on the upper premolars, or very minute. Foreleg slightly shorter than hindleg.

Kenya Rift Valley NW into S Sudan, E of the Nile.

Diceros bicornis longipes Zukowsky, 1949

1949 *Diceros bicornis longipes* Zukowsky. Mogrum, Chad.

A very small subspecies, equivalent in size to *D. b. michaeli*; shorter occipital crest; long distal limb segments;

wide, square base to the horns. Mandibular first premolar retained in the adults. Crochet on the maxillary premolars simple (as in *D. b. brucii*), not bifid (unlike most subspecies); these premolars commonly possessing a crista.

Formerly from SW Chad, Central African Republic (CAR), N Cameroon, and NE Nigeria. Probably extinct.

Microsatellites of a single individual of this subspecies were studied by Harley et al. (2005), who found it more strongly differentiated from the other subspecies he studied than these latter were from each other.

Ceratotherium Gray, 1868

The basic skull characters are as in *Diceros*. The incisors are rudimentary (possibly only deciduous) or absent; the front of both jaws is abbreviated. There is no subaural closure. The occipital plane is narrow, extending backward in lateral view, and overhanging the occipital condyles posteriorly. The nasal bones are much thickened, and truncated anteriorly.

Compared with *Diceros*, the cranium is extremely elongated; the occipital crest is enormously prolonged posteriorly; the dorsal outline of the cranium is still less concave; the protoloph and the metaloph on the upper cheekteeth are strongly curved backward, fusing with wear; the cheekteeth are higher-crowned, with much crown cement; the mandibular symphysis is very broad; the ascending ramus is more backwardly inclined; there is a pre-sacral eminence, formed by the anticlinal status of the 17th or 18th thoracic vertebra; there are two horns, the frontal horn placed somewhat behind the nasal horn; the bases of the two horns rarely touch; the mouth is broad and blunt, with scarcely any median prolongation of the upper lip; there is a muscular nuchal hump; copious subcutaneous fat causes atrophy of the body folds and the costal grooves; the prepuce is translucent, and the penis has eccrine as well as apocrine glands. (Following Groves, 1975b.) Body hair is much reduced, but still detectable in *C. simum*.

Tests on 30 samples from Umfolosi showed that, as far as microsatellites are concerned, there seemed to be a rather low degree of genetic variability, presumably due to the severe population decrease that had occurred by the beginning of the 20th century.

A hybrid between a black rhinoceros male and a southern white rhinoceros female was born in a large enclosure in South Africa, and verified by cytogenetics and microsatellite analysis (Robinson et al., 2005). It was intermediate in head shape between the two; its mouth was more like that of a white rhino, but its ear more like that of a black rhino. To judge by the photos, the shape of the dorsal outline of the body was intermediate between the two parents, and the deep costal grooving was more like that of a black rhino.

Groves et al. (2010) reviewed the differences between northern and southern white rhinos and came to the conclusion that they are strongly distinct species, with about 1 million years of separation. For conservation purposes, this conclusion is especially significant, and it is possible that, had the nature and consistency of the differences between the two been realized earlier (rather than being hidden as "mere subspecies"), more stringent efforts would have managed to save the critically endangered northern species.

Ceratotherium simum (Burchell, 1817)

southern white rhinoceros

1817 *Rhinoceros simus* Burchell.
1827 *Rhinoceros burchellii* Lesson.z
1827 *Rhinoceros canus* Griffith.
1847 *Rhinoceros oswelli* Elliot.
1866 *Rhinoceros kiaboaba* Murray.
1878 *Atelodus simus* var. *camptoceros* Brandt.
1878 *Atelodus simus* var. *prostheceros* Brandt.
The synonymy includes some names elucidated by Rookmaaker (1983).

This is the only species of rhinoceros that today can be considered reasonably "abundant"; it has been widely reintroduced over much of its former range S of the Zambezi, and beyond it (Kenya).

Ceratotherium cottoni (Lydekker, 1908)

northern white rhinoceros

1908 *Rhinoceros simus cottoni* Lydekker.

A very detailed description of this species, a comparison with the southern white rhino, and an argument as to why it has to be considered a distinct species have all recently been given by Groves et al. (2010) and thus will not be repeated here.

It is unfortunate that a study such as this was made only as this species arrived at the brink of extinction; one hopes that the remnants can still be persuaded to breed, and that it will not be "saved" by hybridizing it with *C. simum*.